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Postglacial history of East European boreal forests in the mid-Kama region, pre-Urals, Russia

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The Ural Mountains are an important climatic and biogeographical barrier between European and Siberian forests. In order to shed light on the postglacial formation and evolution of the boreal forests in the European pre-Urals, we obtained a peat sediment core, Chernaya, from the Paltinskoe bog located between the southern taiga and hemiboreal forest zone in the mid-Kama region. We carried out pollen analysis, non-pollen palynomorph analysis, loss-on-ignition tests and radiocarbon dating. Radiocarbon dated records provide centennial to decennial resolution of the vegetation and environmental history of the European pre-Urals for the last 8.8 ka. The postglacial formation of the pre-Uralian hemiboreal forests reveals four important phases: (i) the dominance of Siberian taiga and forest-steppe in the Early Holocene and beginning of the Middle Holocene (8.8–6.9 ka), indicating a dry climate; (ii) the spread of spruce and European broadleaved trees in the Middle Holocene (6.9–4 ka) under wetter climate conditions; (iii) the maximum extent of broadleaved trees coinciding with the arrival and spread of Siberian fir in the Late Holocene (4–2.3 ka); and (iv) the decline of broadleaved trees since the Early Iron Age (2.3 ka – present) possibly due to general climate cooling and logging. While temperate broadleaved trees possibly spread from local refugia in the Urals, fir arrived from Siberia and spread further west. The carbon accumulation rate of Paltinskoe bog (18.9±10.16 g C m^{-2} a^{-1}) is close to the average value of carbon accumulation of northern peatlands. Local development of peat is characterized by non-gradual growth with a phase of intensive carbon accumulation between 3.5 and 2.3 ka. The vegetation was strongly influenced by fire in the Early Holocene and by humans since the Early Iron Age practicing deforestation, agriculture and pasture. Phases of increased anthropogenic activity correlate well with the local archaeological data.

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Stretching from the north to the south, the Ural Mountains are an important climatic barrier as well as a biogeographical contact zone connecting the European with the Siberian flora and fauna. The belt of temperate deciduous forests expanding over the East European Plain (Fig. 1A) loses broadleaved tree species diversity with increasing climate continentality. Starting with species-rich arboreal vegetation with beech (*Fagus sylvatica*), hornbeam (*Carpinus betulus*) and ash (*Fraxinus excelsior*) in the Podolian Upland, the deciduous belt thins out eastwards. Only oak (*Quercus robur*), lime (*Tilia cordata*), elm (*Ulmus glabra* and *U. laevis*), alder (*Alnus glutinosa* and *A. incana*) and hazel (*Corylus avellana*) stretch until the western slope of the Ural Mountains, reaching the eastern limit of their distribution. Here, the temperate deciduous trees spread to the north, mixing with dominant boreal evergreen and deciduous species such as spruce (*Picea obovata*), fir (*Abies sibirica*), pine (*Pinus sylvestris*), birch (*Betula pubescens*, *B. pendula*) and poplar (*Populus tremula*). Across the north–south gradient, their abundance in the boreal forests determines biogeographical zones of mid- and southern taiga, hemiboreal mixed forest, and forest-steppe zone (Bohn *et al.* 2003).

Despite the importance of the Ural Mountains in terms of vegetation patterns, surprisingly little is known about the vegetation history of the eastern edge of continental Europe. In general, palaeoecological studies in the Ural region are rare and concentrated mainly in the northern polar (e.g. Cremer *et al.* 2004; Kultti 2004; Andreev *et al.* 2005; Henriksen *et al.* 2008; Panova *et al.* 2010; Svendsen *et al.* 2014) and southern Ural mountains (e.g. Nemkova 1992; Lapteva & Korona 2012; Stobbe *et al.* 2015). Studies in the middle Urals have been carried out mainly on the eastern slope (Blagoveshchenskiy 1940, 1943; Sukachev & Poplavskaya 1946; Gorchakovskiy 1953; Maslennikova *et al.* 2016; Panova & Antipina 2016), while the vegetation history of the western pre-Ural region is still very poorly studied. Here, studies related to peatland exploration started in the 1920s and 1930s and included pollen analysis sporadically (Gerasimov 1926; Igoshina 1927; Gerasimov 1932; Henckel & Krasovsky 1934; Henckel & Lebedeva 1940; Danilova 1948; Storozheva 1962; Henckel 1974). Lack of radiocarbon dates and low temporal resolution of these records prevent the reconstruction of the postglacial vegetation history of the region. In the later studies, interpretation of pollen data (Elovicheva 1991) is still based on stratigraphy, which is often not supported by radiocarbon dates (Kokarovtsev 1992). More recent studies from the upper Kama region cover the Middle and Late Holocene (Demakov *et al.* 2016; Lapteva *et al.* 2016, 2017, 2019; Zaretskaya *et al.* 2020).

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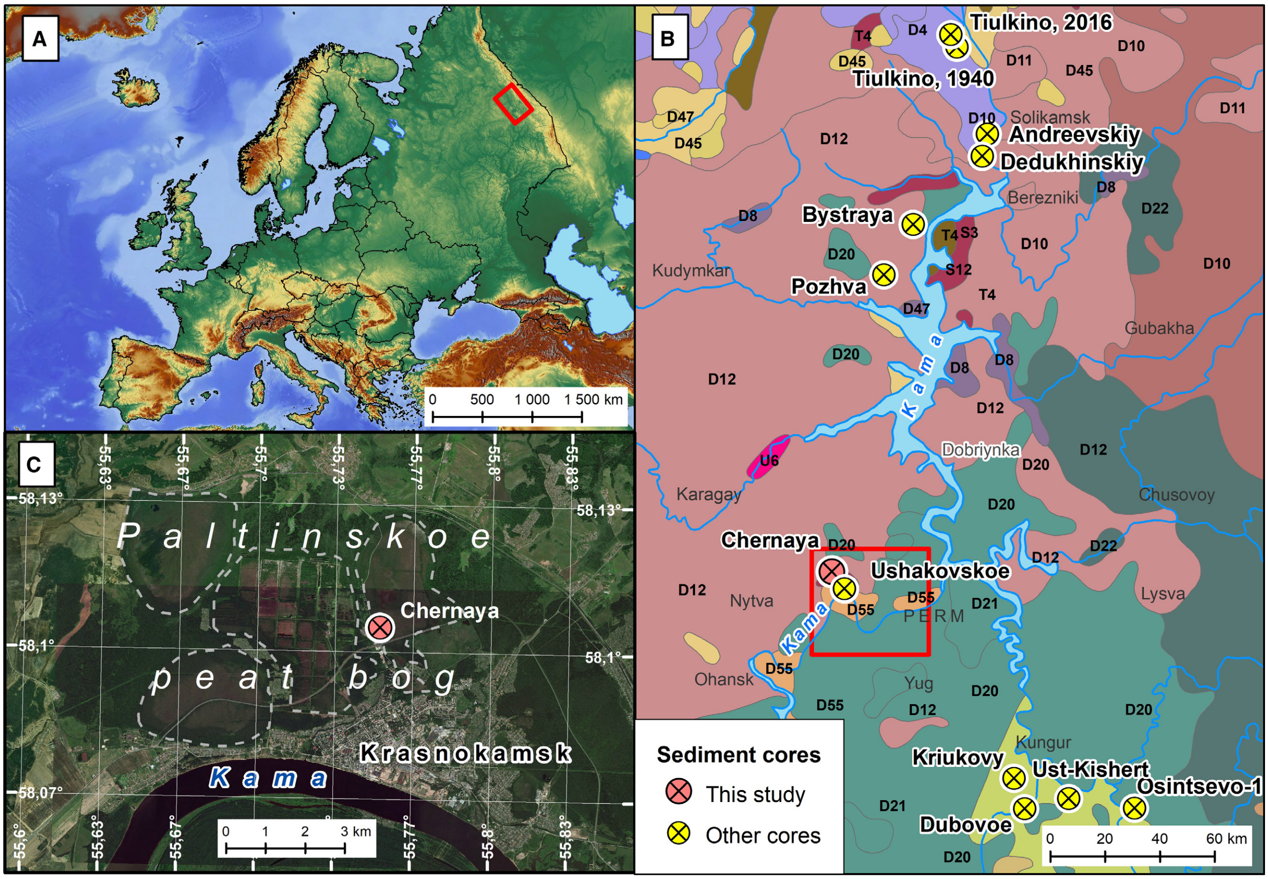

Fig. 1. Maps showing location of the study site, Paltinskoe peat bog. A. Map of Europe. B. Vegetation map of the study region (Bohn *et al.* 2003) with location of sediment cores discussed in the text and rectangle showing the position of Fig. 2. Vegetation units: D4 = north European moss-rich spruce forests; D8 = Scandinavian–east European spruce forests; D10 = pre-Ural fir-spruce forests: D11 = pre-Ural hygrophilous pine-spruce forests; D12 = pre-Ural fir-spruce forests; D20 = pre-Ural herb-rich fir-spruce forests; D21 = pre-Ural herb-rich fir-spruce forests; D22 = middle and south Ural herb-rich spruce-fir forests; D45 = north European pine forests; D47 = north and east European hygrophilous pine forests; D55 = east European psammophytic pine forests; S3 = *Sphagnum fuscum*-raised bogs; S12 = central to east European lowland wooded raised bogs. C. Aerial photograph of Paltinskoe peat bog. [Colour figure can be viewed at www.boreas.dk]

In order to close this gap and shed light on the postglacial formation and evolution of the boreal forests in the mid-Kama region of the European pre-Urals, we obtained a sediment core from the Paltinskoe peat bog (Fig. 1). Here we present the vegetation and environmental history in centennial to decadal resolution reconstructed using pollen and non-pollen palynomorph (NPP) analyses, loss-on-ignition and radiocarbon dating. We investigate the following main aspects: (i) the formation and dynamics of hemiboreal forests during the Holocene; (ii) the role of humans in the formation of the modern landscapes in the mid-Kama region; and (iii) the carbon accumulation of the studied peat bog.

Geographical setting

The climate of the middle Kama region is continental with long, cold and snowy winters and short, warm summers. The average temperature of Perm is 2 °C. January is the coldest month with an average temperature of −14.7 °C. July is the hottest month of the year with an average temperature of 17.9 °C. The precipitation varies between 25–29 mm in February and March and 81 mm in July and the annual mean precipitation is 627 mm. First snow occurs between September and late October and the snow cover lasts 6 to 6.5 months until April. River freezing occurs in early November. Ice persists until early April (Shklyaev & Shklyaeva 2006; Tartakovskiy 2012).

The Paltinskoe bog is located between two main vegetation borders: the southern boreal fir-spruce forests and the hemiboreal fir-spruce forests (Fig. 1B; Bohn *et al.* 2003). The pre-Uralian southern boreal fir-spruce forests consist of *Picea obovata* and *Abies sibirica* with an admixture of *Betula pubescens*, *Populus tremula* and *Tilia cordata*. The relatively open shrub layer contains species such as *Rosa majalis*, *Lonicera xylosteum* and *Sorbus aucuparia*. Two main types of herb layer can be differentiated: dwarf-shrub-rich (mainly boreal species e.g. *Dryopteris dilatata*, *Linnaea borealis* and *Vaccinium myrtillus*) and herb-rich (*Luzula pilosa*, *Pulmonaria obscura* and *Crepis sibirica*). *Pleurozium schreiberi* and *Rhytidiadelphus triquetrus* are typical species of the moss layer. The forests grow on grey-brown podzolic or podzol-like soils with loam or loamy sand texture and moist conditions (Gorchakovskiy 1965; Bohn *et al.* 2003; Ovesnov 2009). The pre-Uralian hemiboreal fir-spruce forests consist of *Picea obovata*, *Abies sibirica*, *Picea obovata* × *abies*, *Tilia cordata* and *Ulmus glabra* dominating the tree layer. *Lonicera xylosteum*, *Viburnum opulus* and *Rubus idaeus* are common in the shrub layer. The herb layer of the hemiboreal fir-spruce forest contains nemoral broadleaved components such as *Lathyrus vernus*, *Asarum europaeum* and *Galium odoratum*. The proportion of nemoral species increases with a north-to-south gradient. *Rhytidiadelphus triquetrus*, *Hylocomium splendens* and *Ptilium crista-castrensis* mainly form the moss layer in these forests (Gorchakovskiy 1965; Bohn *et al.* 2003; Ovesnov 2009).

The Paltinskoe peat bog is located on the ancient terrace of the Kama River, composed of post-Pliocene sands (Henckel 1974). It consists of four large peat bogs (Fig. 1C) with a total area of about 600 ha with an average depth of about 3.63 m (up to 8.5 m). The total volume of peat (40% humidity) is about 29 million m^3 (Verkhoyarov 1976). The Paltinskoe peat bog was drained for turf extraction in 1988, which however was stopped in the 1990s. Today, the Paltinskoe peat bog is surrounded by *Pinus* forests and secondary *Betula-Populus* forests. Furthermore, small areas of the study region are covered by *Picea-Abies* forests and *Ulmus-Tilia* forests. The landscapes to the east, north and west of the peat bog are characterized by large agricultural areas, while urban areas belonging to the city of Krasnokamsk are located to the south (Fig. 1C). The moderate continental climate allows the cultivation of rye, oats, wheat, corn, buckwheat, millet, flax, canola, potatoes, onions, carrots and cabbage.

The coring area is located in a *Sphagnum* peat bog with *Polytrichum communis* assemblages covered by low-growth *Pinus sylvestris* and *Betula pubescens* and shrubs such as *Ledum palustre*, *Andromeda polyflora*, *Vaccinium oxycoccum*, *V. uliginosum*, *Chamaedaphne calyculata* and *Rubus chamaemorus.* The herb layer is dominated by *Carex* spp., *Eriophorum vaginatum*, *Scheuchzeria palustris*, *Drosera rotundifolia* and *Drosera anglica*.

Archaeological and historical background

The middle Kama region has been settled by humans since the Middle Palaeolithic (Melnichuk *et al.* 2011; Pavlov 2013; Golovchansky & Melnichuk 2014). However, evidence has been found of settlements around Paltinskoe peat bog dating from the beginning of the Holocene, characterized by the spread of the late stage of the Mesolithic culture (9th - second half of 8th thousand BCE; Melnichuk *et al.* 2001; Golovchansky & Melnichuk 2014). One of the Mesolithic settlements, Shabunichi, is located on the edge of the Paltinskoe bog (Fig. 2).

The Neolithic is represented in a common cultural system of the Volga-Kama (5th-4th thousand BCE). The sites are located on the low banks of small rivers at a distance of a few kilometres from the valley of the Kama river and its major tributaries. They are represented by the remains of semi-earthen dwellings with side niches at the edges, utility pits and ground hearths. Tools and weapons were made of flint, slate and stone (Golovchansky & Melnichuk 2014; Lychagina *et al.* 2017).

Archaeological sites of the Early Eneolithic stage such as the Novoilyin culture (5th – beginning of 3rd thousand BCE), Bor culture (second half of 4th thousand BCE) and Garinskaya culture (end of 4th – first quarter of the 2nd thousand BCE) characterize the transition to the Early Bronze Age. A population of the Garinskaya culture created a centre of non-ferrous metallurgy in an area of Kama copper sandstones (Golovchansky & Melnichuk 2014; Lychagina *et al.* 2017; Vybornov *et al.* 2019). The Early Bronze Age in the Kama region is represented by archaeological sites of the Turbino–Seima type. Four of the six known objects of this type in the Perm Kama are located near the city of Perm, including the Turbinsky burial (17th–16th centuries BCE) and chronological horizon settlement Zaosinovo VII (16th–14th centuries BCE) located in the left bank of the Kama river near Krasavinskoe bog (Denisov *et al.* 2011; Fig. 2). The Late Bronze Age is represented in the Perm Kama region by the Erzovskaya culture (13th–10th centuries BCE), which evolved from the Zaosinovo VII type.

The most intensive occupation of the study region occurred during the Iron Age. The Early Iron Age culture Ananyino dates from the 9th to the 3rd centuries BCE (Goldina 1999; Koryakova & Epimakhov 2007; Korenyuk 2009). Settlements located along the Kama River include fortresses, open settlements and temporary hunting camps. The houses were constructed out of log wood and the economy of the Ananyino culture was based on metal working, hunting, livestock farming, fishing and gathering (Goldina 1999). Possibly because of the lack of archaeological investigations, settlements of Ananyino culture are not known in the area near Paltinskoe peat bog; however, many Ananyino settlements are located on the left bank of Kama river near Krasavinskoe peat bog. Between the 3rd and 2nd centuries BCE, the Ananyino culture transformed into new cultural horizons such as the Glyadenovo culture, which occupied areas covered by southern boreal and hemiboreal forests of the middle and upper Kama from the 3rd century BCE until the 5th century CE (Goldina 1999; Polyakov 2001; Koryakova & Epimakhov 2007). Pereskokov (2018) mentions 80 fortifications and 357 settlements of the Glyadenovo culture in the area of

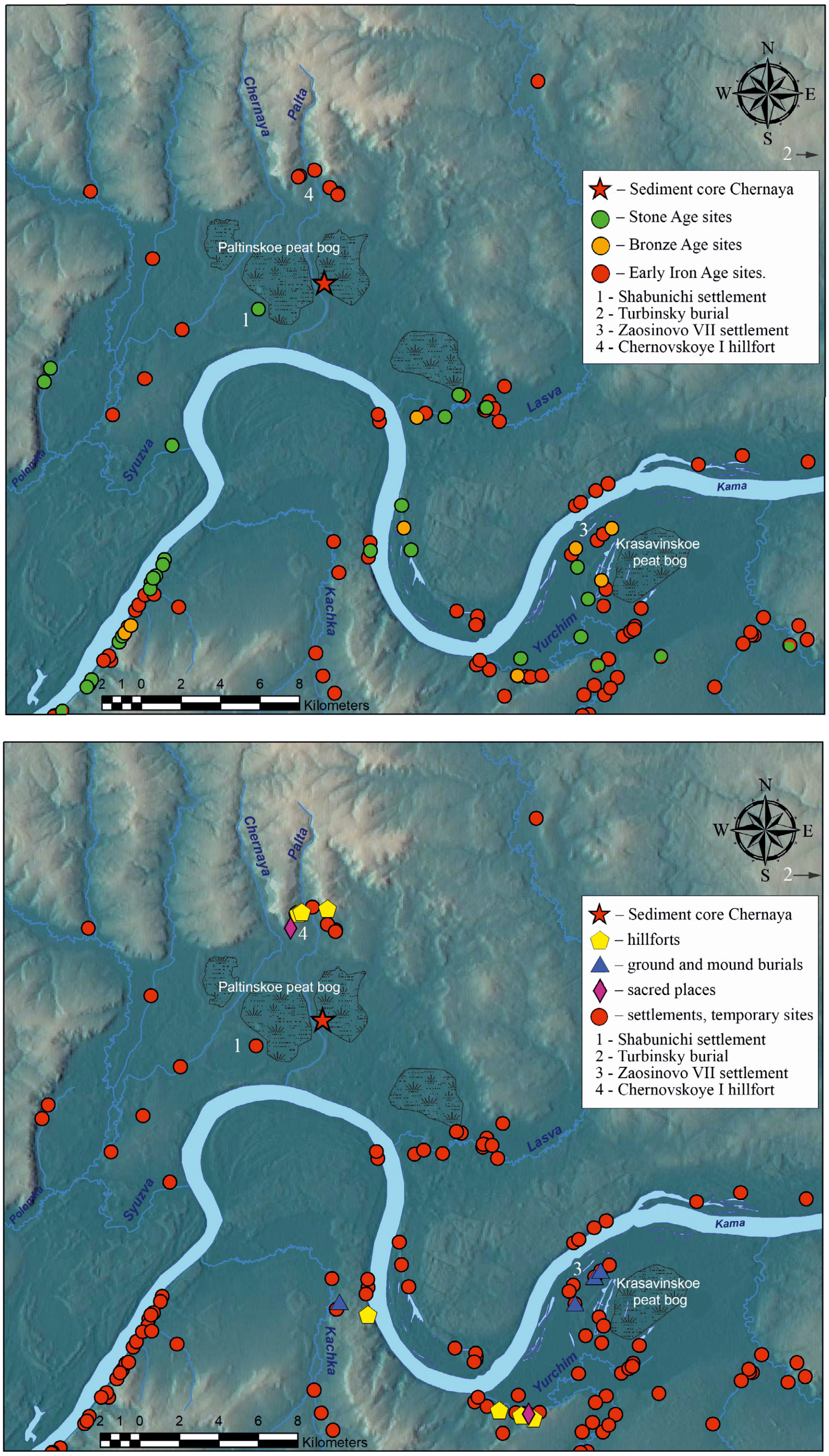

Fig. 2. Archaeological sites of the Paltinskoe peat bog area. A. Chronological position of the sites. B. Type of the sites. [Colour figure can be viewed at www.boreas.dk]

Kama River and its tributaries (Fig. 2). In general, the settlements were located on the river terraces and flood-plains (Polyakov 2001). It is assumed that hunting and animal husbandry were the most important basis of the economy (Schmidt 1927; Pereskokov 2013, 2018). However, the presence of agricultural tools (Pereskokov 2018) and rare findings of cereals (Gening 1959) suggest agriculture. Lack of archaeobotanical investigations hampers the estimation of the role of plants in the diet. A defining character of this culture is the so-called 'kostishche', a sacred place with animal bones (Pereskokov 2018). No systematic zoological analysis has been done yet, but the preliminary data show predominance of domestic animals such as cattle, horses, sheep, goats and pigs (Korenyuk *et al.* 2018). A group of sites of the late period of the Glyadenovo culture, including three hillforts, a sacred 'kostishche' and several villages, is located on the ancient terrace of the Kama river near the Paltinskoe bog. The best studied of them is fort Chernovskoye I (3rd–6th centuries CE), containing the remains of long-term residential buildings and metallurgical production (Oborin 1962). The Glyadenovo culture split into the northern Lomovatovo and southern Nevolino cultural groups between the 5th and 6th centuries CE and left the area.

The lack of archaeological sites suggests that the mid-Kama region was abandoned until the 16th century, when it became a part of the Russian Empire. In the 17th–18th centuries, salt and copper mining industries led to economic development of the Kama region and an increase in the population. Nowadays, large areas of the coniferous und deciduous forests have disappeared, being replaced by agriculture or mining.

Material and methods

Sediment core and age-depth model

The sediment core Chernaya (latitude 58°6′20.23″N, longitude 55°45′8.66″E, altitude 102 m a.s.l.) originates from the Paltinskoe peat bog (Fig. 1C) and is named after the village close to the coring site. The sediment core was obtained in June 2016 from the eastern edge of the peat bog using Russian corer with chambers 50 cm long and 5 cm in diameter. Due to the presence of a tree trunk at 250 cm depth, the entire sediment core (348 cm) was obtained in two sections: 0–250 cm and 250–348 cm, located at a distance of 30 cm from each other. The sediment was packed in plastic tubes and transported to the University of Göttingen, Germany, where it was stored at 4 °C.

For chronology, eight samples of peat and *Betula* bark (Table 1) were dated by the AMS radiocarbon method in the Radiocarbon Laboratory of Poznań (Poland). Calibration of the dates by the IntCal13 calibration curve (Reimer *et al.* 2013) and age-depth model (Fig. 3) was carried out using the clam 2.2 package (Blaauw 2010) in (R Core Team 2020).

To determine the organic content of the core, 69 samples with equal volumes of 1 cm^3 were taken at intervals of every 4 to 5 cm for the loss-on-ignition (LOI) analysis of the sediment core following a standard protocol (Heiri *et al.* 2001). In accordance with the protocol of Chambers *et al.* (2011) peat physical attributes such as bulk density (BD, g cm^{-3}), organic matter content (OC, %) and organic matter bulk density (OMBD, g OM cm^{-3}; also referred to as ash-free bulk density by Loisel *et al.* (2014)) were calculated. The carbon content was estimated by using the average value for northern Holocene *Sphagnum* peat of 42% (Loisel *et al.* 2014) from the top to a depth of 279 cm. Due to changes in the stratigraphy, all samples below 280 cm were calculated by using the value of 51% for non-*Sphagnum* peat (Loisel *et al.* 2014).

Palynological analysis

A total of 83 subsamples of 1 cm^3 were collected at 1 to 10 cm intervals from the sediment core Chernaya. The laboratory treatment included demineralization with cold hydrochloric acid (10%), followed by potassium hydroxide (10%) for 5 min in a water bath, sieving with 200-μm metallic mesh, and acetolysis for 3 min (Erdtman 1960). One tablet of *Lycopodium* spores (Batch number 177745) was added at the beginning of the preparation in order to calculate the concentration of palynomorphs (Stockmarr 1971). Prepared subsamples were stored in glycerine and counted under 400× to 1000× magnification. Counts of at least 500 pollen grains of terrestrial plants per sample (average 583±85) were used for the calculation of percentages. Due to their patchy presence, Cyperaceae as well as water and typical

Table 1. Radiocarbon dates of the sediment cores Chernaya I and Chernaya II.

Lab. no.	Dated material	Depth (cm)	Remarks	Age (^{14}C a BP)	Age (cal. a BP; confidence interval, %)
Chernaya I					
Poz-107817	*Sphagnum* peat	70		1545±30	1373–1525 (95)
Poz-111285	*Sphagnum* peat	98	0.6 mg C	2220±30	2153–2279 (76.4), 2281–2322 (18.3)
Poz-107818	*Sphagnum* peat	120	0.1 mg C	2390±50	2336–2540 (74.7), 2564–2574 (0.9), 2586–2617 (5.2), 2632–2699 (14.2)
Poz-111290	*Sphagnum* peat	180		2970±30	3008–3012 (0.5), 3031–3049 (1.9), 3057–3229 (92.5)
Poz-83580	*Eriophorum* peat	240		3310±35	3455–3614 (94.1), 3626–3630 (0.8)
Chernaya II					
Poz-111286	*Sphagnum* peat	265		3895±35	4185–4185 (0.1), 4193–4195 (0.3), 4235–4422 (94.5)
Poz-111291	*Sphagnum* peat	315	0.8 mg C	5940±30	6675–6804 (83.1), 6813–6849 (11.9)
Poz-100973	*Betula* bark	330		6935±35	7684–7839 (95)

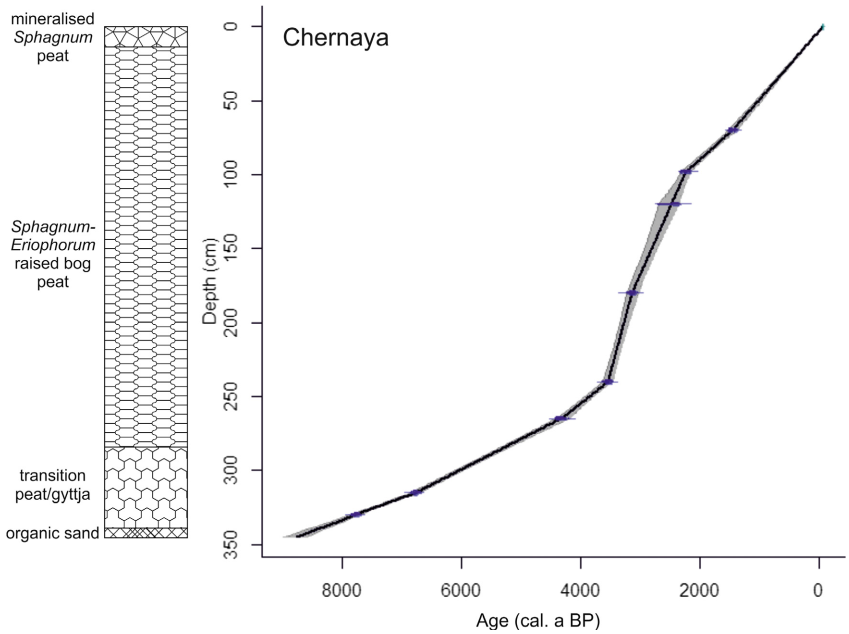

Fig. 3. Age-depth model and simplified stratigraphical column of the sediment core Chernaya from Paltinskoe peat bog. [Colour figure can be viewed at www.boreas.dk]

peat bog pollen taxa were excluded from the base sum. Pollen identification and taxonomy follows Beug (2004) and Moore *et al.* (1999). Beside pollen and plant spores, non-pollen palynomorphs (NPP) and charcoal particles were counted. For NPP identification, we used the NPP database http://nonpollenpalynomorphs.tsu.ru/. Pollen and NPP are expressed as percentages of the total sum of terrestrial pollen. The diagrams were constructed using C2 version 1.5.6 (Juggins 2007). The diagram was zoned by a visual inspection based on major changes in pollen assemblages and indicative pollen taxa.

Results

Stratigraphy, age-depth model and peat properties

The sediment core has three distinctive stratigraphical units (Fig. 3). A sandy organic layer at the bottom (345–348 cm) is followed by a unit of well-decomposed peat/gyttja (279–345 cm) with black (possibly charcoal) layers at 279–282, 286, 297, 334, 343 cm and a white layer of *Betula* bark at 330 cm. The upper unit (0–279 cm) consists of a poor to moderately decomposed *Sphagnum* peat with *Eriophorum vaginatum* remains. The upper 12 cm of the peat is mineralized, reflecting the influence of the recent drainage of the peat.

The age-depth model (Fig. 3) shows considerable changes in sedimentation rates through time. In the lowest part of the core (345–240 cm, ~8.8–3.5 ka), the sedimentation rate slowly increases from 0.15 to 0.3 mm a^{-1}. At 235 cm (~3.5 ka), the rate increases to 1.5 mm a^{-1} and remains as high until ~3 ka (175 cm), slightly decreasing after to 0.9 mm a^{-1}. At 95 cm (~2.1 ka) the sedimentation rate drops to 0.36 mm a^{-1}, then increases slightly to 0.45 mm a^{-1} at 65 cm (~1.3 ka).

The results of the LOI measurements (Fig. 4) show that the lower part of the sediment (345–335 cm) contains 41 to 78% of organic matter, which then increases at 330 cm (7.8 ka) to 95%. The first drop in organic content to 88% occurs at ~4 ka (255 cm), increasing again to 97–99% at 251 cm (3.9 ka). Between 220 and 80 cm (3.4–1.2 ka) organic content varies between 80 and 96%. It then stabilizes again until the upper 10 cm, after which it drops to 55%.

Bulk density (BD) values vary between 0.04 and 0.44 g cm^{-3} with an average value of 0.09±0.05 g cm^{-3}. The highest value occurs ~8.7 ka and the lowest ~3.2 ka. The most rapid change is displayed between ~8.5 to ~8 ka (0.44 g cm^{-3} decreases to 0.07 g cm^{-3}). Periods of generally higher values occur between ~7.7 to ~5.5 ka (mean value: 0.14±0.02 g cm^{-3}) and during the last ~100 years (mean: 0.16±0.02 g cm^{-3}). A period of low BD values occurs between ~4.5 to ~2.2 ka (mean: 0.07±0.01 g cm^{-3}).

The carbon accumulation rate (CAR) calculated on the basis of LOI ranges between 3.05 and 53.05 g C m^{-2} a^{-1} (mean: 18.9±10.16 g C m^{-2} a^{-1}). The lowest CAR of ~3–9 g C m^{-2} a^{-1} occurs at ~8, ~4.7 to ~3.5, and ~1.9 to ~1.7 ka. Noticeable alternations with highest rates of accumulated carbon appear between ~3.5 and ~2.2 ka (18–53 g C m^{-2} a^{-1}).

Palynological analysis

Based on the age-depth model, the temporal resolution of the pollen diagram varies between 43 and 244 years,

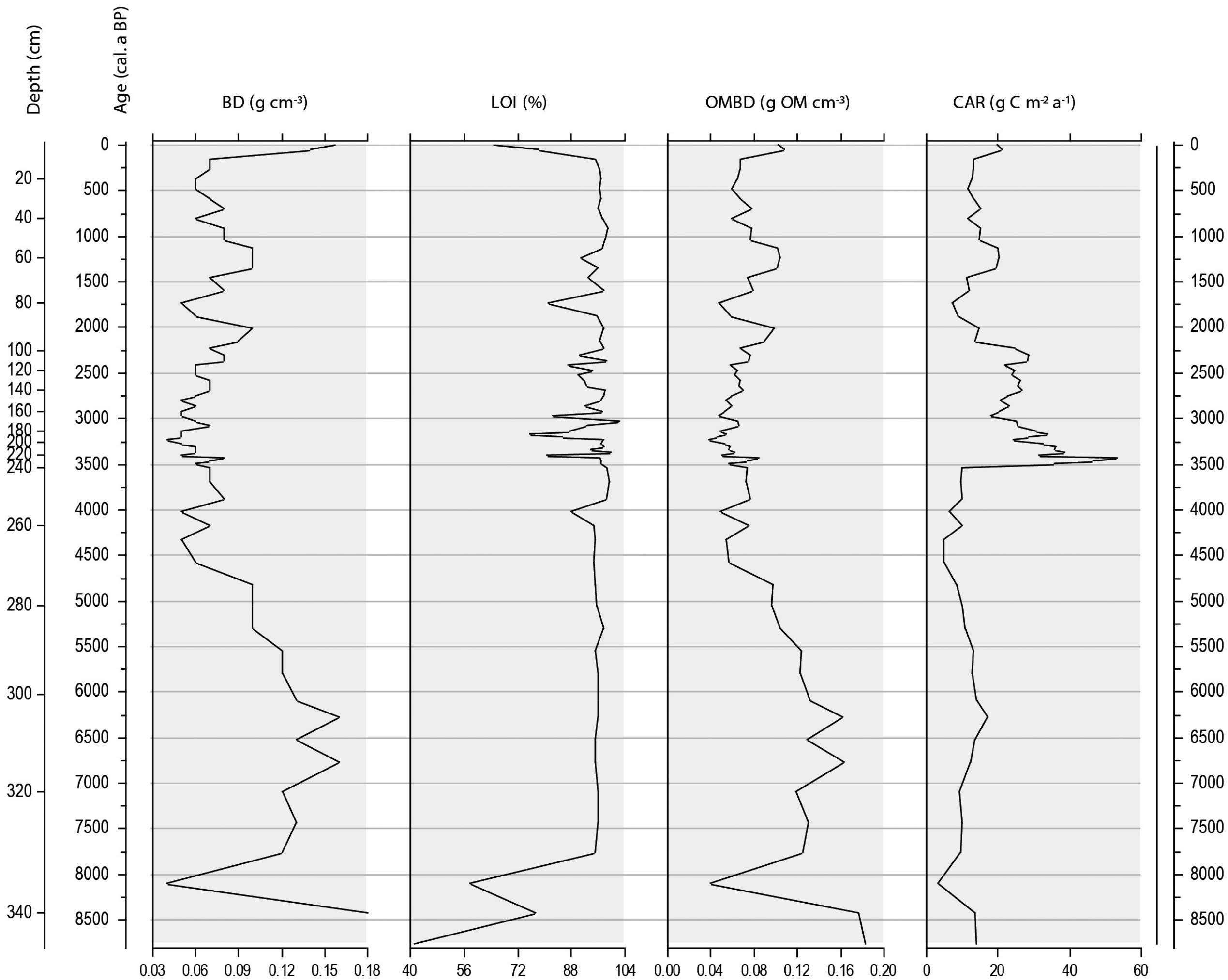

Fig. 4. Overview of peat properties: bulk density, loss on ignition at 550 °C, organic matter bulk density and carbon accumulation rate.

representing the vegetation history record on a decennial to centennial scale. In total, 87 pollen types and 83 NPP types were identified. Based on major changes in pollen composition, the pollen diagram (Figs 5–7) is divided into five local pollen zones (LPZs).

LPZ-1 (345–337 cm, 8.8–8.2 ka) is characterized by a dominance of *Pinus diploxylon*-type (68%), *Betula pubescens*-type (21%) and *Picea* (14%) with the presence of *Pinus haploxylon*-type, *Larix* and *Juniperus*. Non-arboreal pollen (NAP) is represented mainly by *Artemisia*. High values of fern spores, *Equisetum* spores and HdV-128 are typical. Charcoal concentrations are high with a burning horizon at 340 cm (~8.4 ka) and presence of conifer charcoals.

LPZ-2 can be subdivided into two subzones. LPZ-2a (337–327 cm, 8.2–7.6 ka) shows an increase in Poaceae (11%), Cyperaceae (24%) and *Betula pubescens*-type (67%). Percentages of *Pinus diploxylon*-type (30%) and *Picea* (6%) decrease considerably. Fern spores decrease, while the *Sphagnum* spore maximum appears. NPP spectra show the presence of the decomposing/coprophilous fungi *Coniochaeta ligniaria*, *Gelasinospora* and *Podospora inflatula*-type. Charcoal concentrations remain high throughout.

In LPZ-2b (327–317 cm, 7.6–6.9 ka), *Pinus diploxylon*-type increases (42%) and *Alnus*, *Ulmus* and *Corylus* occur regularly. Poaceae, Cyperaceae and fern spores decrease. Charcoal concentrations are high with a maximum at 324 cm and the appearance of charred pollen.

LPZ-3 (317–255 cm, 6.9–4 ka) is characterized by the arboreal pollen (AP) maximum, reaching 99%. The lower boundary is drawn at the *Tilia* onset and start of a gradual increase in temperate trees *Alnus*, *Ulmus*, *Quercus*, *Corylus* upwards. *Picea* increases gradually up to 21%, while *Betula pubescens*-type decreases through the zone from 71 to 38%. NPP spectra are poor and dominated by pollen with hyphae and rare occurrences of *Sordaria*, *Sporormiella* and *Coniochaeta ligniaria*. At the end of the zone, *Sphagnum* spores and sphagnophi-

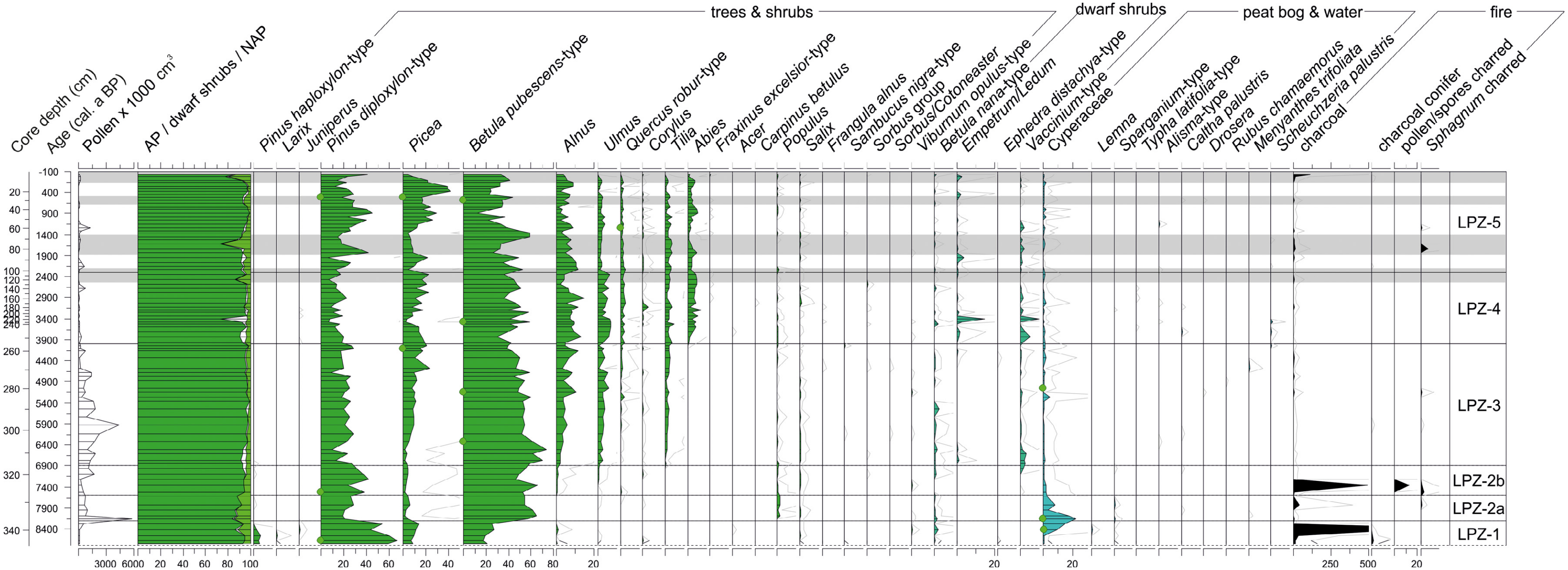

Fig. 5. Pollen diagram of the sediment core Chernaya representing arboreal pollen, pollen of peat bog and water plants and charred particles. [Colour figure can be viewed at www.boreas.dk]

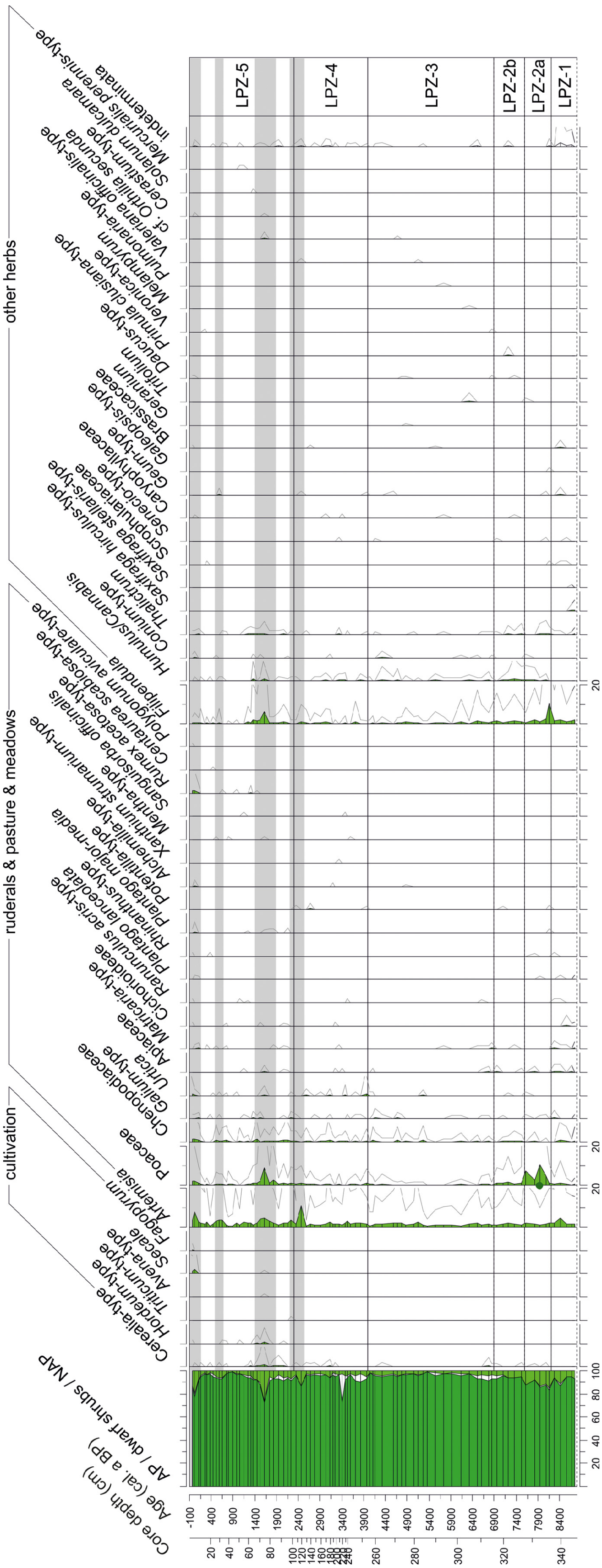

Fig. 6. Pollen diagram of the sediment core Chernaya representing non-arboreal pollen (selected curves). [Colour figure can be viewed at www.boreas.dk]

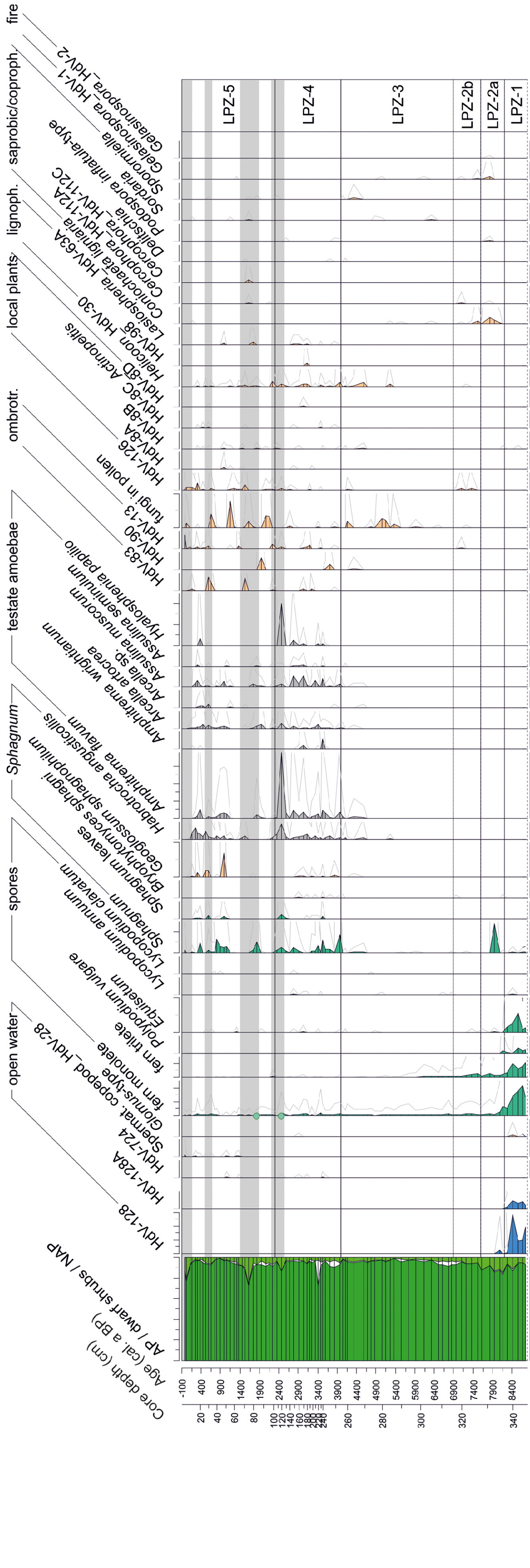

Fig. 7. Non-pollen palynomorph (NPP) diagram of the sediment core Chernaya (selected curves). ombrotr. = ombrotrophic; lignoph. = lignophilous; coproph. = coprophilous. [Colour figure can be viewed at www.boreas.dk]

lous assemblages are present. Charcoal concentrations are low.

The lower boundary of LPZ-4 (255–105 cm, 4–2.3 ka) is identified by the onset of the *Abies* curve, reaching a maximum of 7%. Temperate trees *Alnus*, *Ulmus*, *Tilia* and *Quercus* also reach their maxima. High values of *Artemisia* at 240 cm (3.5 ka) and 120 cm (2.5 ka) occur together with an increase in Poaceae and *Urtica*. From 3.2 ka, Cerealia-type increase. *Sphagnum* spores and leaves, and a wide range of testate amoebae including *Amphitrema flavum* and *A. wrightianum*, *Habrotrocha angisticollis* and *Geoglossum sphagnophyllum* are present, varying in abundance in the zone.

A sharp decrease in *Abies* and *Ulmus* below 2% and a gradual decrease in *Alnus*, *Tilia* and *Quercus* define the lower boundary of LPZ-5 (105–0 cm, 2.3 ka–present). Four maxima of *Betula pubescens*-type, *Artemisia*, Poaceae, Cerealia-type and *Filipendula* correlate with increased charcoal. These phases alternate with phases of increase in *Picea*, *Abies* and *Pinus*. The top sample is characterized by presence of *Fagopyrum* and diverse assemblages with Cichorioideae, *Plantago major-media*, *Ranunculus acris*-type, *Rumex acetosella*-type, *Polygonum aviculare*-type. *Sphagnum* spores and sphagnophilous assemblages vary.

Interpretation

Regional vegetation history

The regional vegetation history is well reflected in the pollen diagram for the Chernaya sediment core from the Paltinskoe peat bog. The first zone LPZ-1 reveals the presence of open boreal forests dominated by *Pinus sylvestris*, *Betula* and *Picea* with *Larix* and *Pinus sibirica*. High charcoal concentrations suggest frequent/strong fire events.

After 8.2 ka, an increase in Poaceae and *Betula pubescens*-type and simultaneous decrease in *Pinus* and *Picea* (LPZ-2a) suggest that the landscapes were possibly covered by forest-steppe with grasslands and open birch and pine forests. NAP values reaching 16% are very high for the boreal forest (compare with Novenko *et al.* 2018). Such high values are comparable to open vegetation conditions during the Lateglacial (e.g. Elovicheva 1991) or anthropogenic impact in the Late Holocene (Figs 5–7). This argument together with the dominance of Poaceae and diverse NAP taxa such as *Artemisia*, *Plantago lanceolata*, *Plantago major-media*, *Potentilla*, *Ranunclulus acris*-type, *Matricaria*-type and *Senecio*-type might indicate open grassland with forest patches (grass forest-steppe). Dry local conditions are also evidenced by decreases in CAR and BD during this time (see next section). Most likely, the dry 8.2 ka event was a trigger for such noticeable vegetation changes, lasting for ~600 years. Alternatively, Mesolithic settlement at the Paltinskoe peat could be the reason for deforestation and creation of open landscapes; however, the lack of radiocarbon dates prevents detailed comparison of the phases. From 7.6 ka, climatic conditions were getting milder, allowing the spread of *Picea* and arrival of temperate trees such as *Ulmus*, *Alnus* and *Corylus* in the open forest-steppe landscapes (LPZ-2b). Large amounts of charcoal including charred pollen and *Sphagnum* leaves (Fig. 5) indicate frequent/intensive local fires.

From 6.9 ka, the spread of spruce with admixture of temperate trees such as *Ulmus*, *Tilia*, *Quercus* and *Corylus* (LPZ-3) indicates the formation of hemiboreal forests. Increasing percentages of *Alnus* reveal the development of alder wetlands in the region. The establishment of the hemiboreal forests with spruce indicate wetter climate conditions, which also might reduce the fire frequency.

The next considerable change in the vegetation composition occurred at around 4 ka and is indicated by the arrival and spread of *Abies* (LPZ-4). From this point, we can say that the formation of the modern hemiboreal forests in the region began. At the same time, an increase in anthropogenic indicators such as *Urtica*, *Artemisia*, Poaceae and Cerealia-type show an increasing influence of humans on the vegetation.

Around 2.3 ka, a distinctive decrease in *Picea*, *Ulmus* and *Abies* values (LPZ-5) indicates reduction of these species in the vegetation cover. This could have either climatic or anthropogenic causes, or both. The former explanation is supported by the simultaneous decreases in the values for these species and by a dry phase in peat development (see the next section). The latter explanation is supported by an stronger increase in anthropogenic indicators such as *Artemisia*, Poaceae, Cerealia-type and *Plantago major-media* and in charcoal concentrations (see Discussion).

Four phases of increased anthropogenic activities are reflected in the pollen diagram by the increase in *Artemisia*, other ruderal herbs, the pioneer *Betula pubescens*-type and charcoal. The first phase between the 6th and 3rd centuries BCE corresponds to Ananyino culture, the second phase (1st–6th centuries CE) – Glyadenovo culture, the third phase (13th–15th centuries CE) – Rodanovo culture (?), and the last (18th–20th centuries CE) to Russian colonization. These four phases alternate with phases of recovery of spruce, pine and fir. In contrast, temperate trees do not reach the same cover as before, but decline further especially during the last millennium, possibly due to the general Late Holocene cooling trend. This process led to the establishment of the present border between the southern taiga and the hemiboreal forest zone (Fig. 1B). The most recent strong impact on the vegetation occurred in the last 300 years and is correlated with Russian colonization and the Soviet Period, indicated by presence of *Fagopyrum* and an increase in further anthropogenic indicators such as *Ranunculus acris*-type, *Rumex acetosa*-type and *Polygonum aviculare*-type.

Peat bog development

Accumulation of organic matter and development of the mire at the coring site started at about 8.8 ka. High amounts of HdV-128 indicate the presence of a meso- to eutrophic shallow water body (van Geel 1978), while the presence of fern, *Equisetum* and *Sphagnum* spores indicates the development of wetlands in the surrounding areas. The groundwater level might have increased at this time leading to surface water stagnation, favouring mire development. The BD peaks at ~8.7 ka during development of wetland what is related to the fen vegetation.

BD as well as CAR strongly decrease at ~8 ka, correlating to a dry phase of forest-steppe establishment (Fig. 5). During a time of milder conditions and the formation of forests with temperate trees around the mire, BD increases (~7.7 to ~5.5 ka). Consequently, due to higher temperatures, the production of vascular plant material also increases.

Although a *Sphagnum* spore maximum occurs at ~8 ka, the establishment of the *Sphagnum* peat and its further development starts at ~4.3 ka, which is supported by the occurrence of typical peat bog indicators such as *Amphitrema flavum*, diverse testate amoebae, *Habrotrocha angusticollis* and the presence of *Sphagnum* spores and leaves. Maxima in BD and CAR values between ~3.5 and 2.3 ka occur during the strong increase in peat accumulation rates (Fig. 3), indicating a wet and warm period with considerable *Sphagnum* peat development.

The peat bog development was interrupted by two long dry phases between 2.3–2 ka and 1.6–1.2 ka, indicated by a decrease in *Sphagnum*-associated assemblages and an increase in pollen covered by fungal hyphae (Fig. 7), indicating stronger decomposition and mineralization of the peat by ectomycorrhizal or ericoid mycorrhizal fungi (Shumilovskikh *et al.* 2015). Furthermore, a decrease in peat accumulation rate (Fig. 3) and decrease in CAR (Fig. 4) evidence slower peat growth. After 1.3 ka, peat accumulation and CAR increase and *Sphagnum* indicators occur again, indicating further accumulation of the peat bog. Drainage for commercial use around 30 years ago may have resulted in increasing values of BD due to the decreasing water table.

Discussion

Formation of the pre-Uralian hemiboreal forests in the Holocene

The late Early Holocene vegetation history reveals landscapes covered by open pine-birch-spruce forests similar to the recent southern taiga of the Siberian type. Such vegetation is now found under the more continental climate of the eastern slope of the mid-Urals and further in the western Siberia (Gerasimov 1964). Our interpretation is supported by the pollen record Osintsevo-I from the southern Perm region (Fig. 1), covering the Early and Middle Holocene (Elovicheva 1991). A forest-steppe phase at the beginning of the Middle Holocene represents a vegetation of Siberian type dominated by birch and patches of pine and spruce. Today, such vegetation can be found in the eastern part of the southern Urals (Gerasimov 1964).

Change to European hemiboreal forests with spruce and temperate trees occurred gradually with a stepwise arrival of alder, elm, hazel, oak and finally lime. The origin of temperate trees in the mid-Urals is an open question. Two contradictory hypotheses are considered by geobotanists: (i) the spread of temperate trees occurred from the local glacial refugia (Kats 1962; Gorchakovskiy 1965; Ovesnov 2009), or (ii) the Holocene deciduous forests arose primarily from refugia in SE Europe, the eastern Carpathian Mountains and the Podolian upland by long-distance migrations (Ponomarev 1948; Gorchakovskiy 1953; Bohn *et al.* 2003). Our data show a sporadic occurrence of pollen of elm, alder, hazel and oak after 8.8 ka. However, all these species are wind-pollinated and their rare occurrence can be explained by long-distance transport. If we take a continuous curve as an indicator of presence of the trees in the surrounding area (Kats 1962), the arrival of broadleaved trees to the mid-Kama region should occur in the Middle Holocene: *Alnus* at 7.5, *Ulmus* at 7.2, *Tilia*, *Quercus* and *Corylus* after 6.8 ka. The latter shows a disrupted curve suggesting that hazel possibly never established close to the Paltinskoe peat bog but was rather present in the southern regions where it grows now. The timing of spread of broadleaved trees in the southern taiga and hemiboreal forests in Paltinskoe is comparable to that in the western part of the East European Plain after ~8 ka (Novenko *et al.* 2009, 2016), suggesting that spread of broadleaved species in the pre-Urals occurred from the local glacial refugia and supporting the first hypothesis.

In terms of formation of the modern dark taiga in the pre-Urals, the final arrival of fir at 4 ka is intriguing. On the East European Plain, only *Abies sibirica* is present as part of the spruce-fir forest. The modern distribution of *Abies sibirica* covers a vast area from 40°E in the East European Plain to 127°E in eastern Siberia and from 45–47°N in the south to 66°N in the north. Its northern distribution is limited by permanent or temporary permafrost zones (Krylov *et al.* 1986). Fir is more shade-tolerant and prefers less continental climatic conditions and more nutrient-rich and well-drained soils in comparison to spruce (Gorchakovskiy 1953; Degteva & Dubrovskiy 2009). The ecological requirements of fir are more similar to broadleaved trees than to spruce (Krylov *et al.* 1986). *Abies sibirica* pollen grains are large and heavy; therefore, they are underrepresented in the pollen spectra (Krylov *et al.* 1986; Poska & Pidek 2010; Pidek *et al.* 2013). Using thresholds of 1%, we estimate the presence of fir within 1 km from the coring site at ~4 ka and within 0.5 km at ~3.8 ka. An application of a characteristic source area of *Abies alba* pollen (Poska & Pidek 2010) to *Abies sibirica* suggests the presence of fir in the vegetation at ~300 m from the sampling point at ~3.5 ka.

The late arrival of fir to the Kama region was already noted in previous studies (e.g. Gerasimov 1926; Golubeva 1956). The more recent pollen records provide a rather heterogeneous picture. In the northern Urals, *Abies* pollen are lacking in the tundra record over the last 40 ka (Svendsen *et al.* 2014) and at the arctic tree line (Kultti 2004) but present at the alpine tree line of the polar Urals during the Holocene. There are sporadic fir pollen records in tundra (Andreev *et al.* 2005), forest-tundra (Panova *et al.* 2010) and in northern taiga close to the Urals (Kultti 2004) but no *Abies* pollen in more western sites (Henricksen *et al.* 2008). In the southern Urals, there are sporadic records of *Abies* pollen in the forest-steppe during the Holocene (Lapteva & Korona 2012) but none in the steppe (Stobbe *et al.* 2015). Regular but rare presence of *Abies* in the northern and southern pollen records may be explained by long-distance transport. On the eastern slope of the middle Urals, *Abies* pollen increases (Panova & Antipina 2016) or appears (Maslennikova *et al.* 2016) in southern pine taiga after 4.3 ka. On the western slope, *Abies* occurs in hemiboreal forest at ~4 ka (this study), and in the middle taiga it is permanently present after 3.8 ka (Demakov *et al.* 2016; Lapteva *et al.* 2017; Zaretskaya *et al.* 2020). Dated pollen records are scarce, but those that exist support the idea of the westward spread of fir from Siberia (Gorchakovskiy 1953). Most probably the main migration corridor was located in the lowlands of the middle Ural Mountains within the zone of southern taiga/hemiboreal forests, from where *Abies* spread later to the north and the south.

It is possible that several factors played a role in the establishment of fir populations and its further spread in the region. First of all, the late spread of fir in the East European Plain can be explained by weak dispersal mechanisms of fir and the long distance to the Siberian refugium. Presence of favourable climate and soil 3000 years earlier is indicated by the spread of broadleaved trees in the study area. However, it took a few millennia for fir to arrive in the region. The second factor is climate, as the period of *Abies* arrival can be characterized by dynamic changes in the ecosystems between 4 and 3.5 ka in the Paltinskoe peat bog. An increased peat growth phase and spread of broadleaved trees indicate warmer and wetter climate conditions, possibly favourable for fir. For the further spread of the populations, an increasing human impact at this time and a strong decrease in *Picea* could have been important, because weak disturbance and a decrease in competition might have played a role in the establishment of the first fir populations. However, we should mention that fir requires a closed canopy for growth and is very sensitive to frost and sun in open landscapes (Krylov *et al.* 1986). Therefore, disturbance regime should have been moderate.

In summary, the postglacial formation of the pre-Uralian hemiboreal forests in terms of tree species arrival reveals three important biogeographical phases in the mid-Kama region: (i) the dominance of Siberian taiga and forest-steppe in the Early and the beginning of the Middle Holocene (8.8–6.9 ka), (ii) the spread of spruce and European broadleaved trees in the Middle Holocene (6.9–4 ka), and (iii) the maximum extent of broadleaved trees coinciding with the arrival and spread of Siberian fir in the Late Holocene (4–2.3 ka). The most recent phase in vegetation development (2.3 ka – present) is related to human activities.

Human impact in the mid-Kama region

While the territory around the Paltinskoe peat bog has been settled since the Mesolithic (Fig. 2), palynological data indicate an increased anthropogenic impact on the vegetation since ~4 ka. The spread of the ruderal plants *Artemisia*, Chenopodiaceae, *Urtica* and *Ranunculus acris*-type indicates opening of the vegetation, possibly by deforestation, while spores of the coprophilous fungi *Sporormiella*, *Podospora inflatula*-type and *Sordaria* suggest the presence of dung, which could be related to livestock grazing. This increase can be attributed to the end of the Eneolithic Garinskaya culture (end of 4th - first quarter of the 2nd thousand BCE), which had its centre of non-ferrous metallurgy in the middle Kama (Golovchansky & Melnichuk 2014; Lychagina *et al.* 2017; Vybornov *et al.* 2019). Furthermore, the Early Bronze Age culture of the Turbino–Seima type is represented by settlements from the 17th to 14th centuries BCE on the left bank of the Kama river near Krasavinskoe bog (Denisov *et al.* 2011; Fig. 2).

A continuous Cerealia-type curve suggesting possible presence of agriculture in the region starts at ~3.2 ka and corresponds to the Late Bronze Age (Koryakova & Epimakhov 2007), represented by the Erzovskaya culture (13th–10th centuries BCE). However, pollen of Cerealia-type can be produced by wild grasses (Beug 2004); therefore, this indicator should be interpreted with caution. Unfortunately, the lack of archaeobotanic investigations in this region prevents a comparison of the palynological evidence of agriculture with archaeological data.

The next period, characterized by a maximum of anthropogenic indicators, occurs between 2.5 and 1.4 ka (550 BCE–600 CE), indicating a long phase of increased human influence during the Early Iron Age. Within this period, two phases of stronger impact from the 6th–3rd centuries BCE and 1st–6th centuries CE are visible, corresponding with the late Ananyino and Glyadenovo cultures, respectively. Although archaeological sites of the Ananyino culture in the Paltinskoe bog surroundings

Table 2. Published long-term carbon accumulation rates CAR and ranges (mean and standard deviation if provided).

Study area	Average long-term CAR	Range of CAR values	Reference
Northern peatlands (mean)	24.1 $g\,C\,m^{-2}\,a^{-1}$	–	Lavoie *et al.* (2005)
	18.6±10.16 $g\,C\,m^{-2}\,a^{-1}$	–	Yu *et al.* (2009)
	23±2 $g\,C\,m^{-2}\,a^{-1}$	–	Loisel *et al.* (2014)
European Russia	21.5 $g\,C\,m^{-2}\,a^{-1}$	8–62 $g\,C\,m^{-2}\,a^{-1}$	Payne *et al.* (2015)
	18.9±10.16 $g\,C\,m^{-2}\,a^{-1}$	3.05–53.05 $g\,C\,m^{-2}\,a^{-1}$	Present study
Southeast Europe	23±14 $g\,C\,m^{-2}\,a^{-1}$	7.1–105.3 $g\,C\,m^{-2}\,a^{-1}$	Panait *et al.* (2017)
Northwest Europe	4–72.5 $g\,C\,m^{-2}\,a^{-1}$	–	Anderson (2002)
Northern Europe	26.1 $g\,C\,m^{-2}\,a^{-1}$	2.8–88.6 $g\,C\,m^{-2}\,a^{-1}$	Tolonen & Turunen (1996)
Canada	16.2 $g\,C\,m^{-2}\,a^{-1}$	–	van Bellen *et al.* (2011)

have not yet been found, the pollen record strongly suggests their presence, highlighting the need for further archaeological investigations in the region. In general, the period between the 6th and 3rd centuries BCE is known for the Ananyino colonization of the tributaries of the Kama river including the Krasavinskoe peat bog (Fig. 2) and the pollen signal strongly indicates the presence of these activities.

In contrast to Ananyino, numerous sites of the Glyadenovo culture are known around the Paltinskoe peat bog (Fig. 2). The closest site, Chernovskoe-I, was active between the 3rd and 6th centuries CE with a maximum of finds in the 4th century CE. During the 4th century CE, the maximum of Cerealia-type pollen exceeds 1%, suggesting possible arable fields of the Glyadenovo culture in the proximity of the coring site. Agricultural practices in Glyadenovo were already suggested from the variety of agricultural tools such as iron and bone mattocks and tools for cereal preparation such as mealing stones and pounders (Pereskokov 2018). Beside undetermined Cerealia-type, several grass types were identified for this period including *Hordeum*-type, *Triticum*-type, *Secale* and *Avena*-type. This is in line with a single finding of cereals in the Osinskoe fortification (Gening 1959), which included *Triticum dicoccum*, *T. aestivum*, *Hordeum vulgare* and *Avena*. Considering forests, the strong decrease in spruce, fir and elm and, in contrast, abundant oak and lime may indicate selective deforestation. Unfortunately, there are no studies on anatomical wood identification from the archaeological sites in the Perm region. The single identification from the Mokino burial (late period of Glyadenovo culture, 3rd–6th centuries CE) shows the use of pine as timber wood (identification by M. Schmidt and S. L. Jahnk). The charcoal maximum indicates increased fires, possibly caused by humans from nearby settlements. Also interesting is an increase in *Alnus* and *Filipendula* (Figs 5, 6), indicating a possible spread of alluvial meadows that could be used for pasture. As suggested by Polyakov (1967), alluvial pastures were one of the most important reasons for the location of Glyadenovo settlements in the alluvial plain. The decrease in Glyadenovo culture activities correlates with the start of a wet phase in the Paltinskoe peat bog development. This observation is in line with a suggestion of Pereskokov (2018) that Glyadenovo populations left the mid-Kama region due to a change in hydrological conditions possibly triggered by climate.

The next maximum of anthropogenic indicators is documented in the 13th–15th centuries. This period is not documented by archaeological sites close to Paltinskoe bog due to poor investigations. In general, during this period the southern Permian territory was under the influence of the Volga Bulgaria. Fur trade from the northern territories to trade centres is known from this time. One of the largest and biggest trade centres was the Rozhdestvenskoe fortification located on the Obva river (Belavin & Krylasova 2008). The closest connection to this centre from the Paltinskoe peat bog is the Syuzva river (Fig. 2). It is possible to suggest the presence of settlements there. The palynological record from the Chernaya sediment core reveals moderate human activities during this period with livestock keeping, small-scale agriculture and felling of spruce and pine, leading to the formation of secondary birch forests. The presence of agriculture at the Rozhdestvenskoe fortification is evidenced by the pollen record (Lapteva *et al.* 2016, 2019). Archaeobotanical investigations (Trofimova *et al.* 2016) reveal the use of *Hordeum vulgare*, *Triticum dicoccum*, *T. aestivum*, *Avena sativa* and *Secale cereale* for cooking. The presence of spikelets of barley indicates local agriculture.

The last maximum of anthropogenic indicators characterizes the last 200 years. It indicates deforestation of spruce, spread of secondary birch forests, increased fire, agriculture with rye, barley and buckwheat in the region as well as the spread of open habitats with ruderal plants such as *Artemisia*, *Plantago major-media*, *Rumex acetosella*-type, *Polygonum aviculare*-type, *Ranunculus acris*-type, *Urtica* and Cichorioideae. This period corresponds to the late Russian colonization starting with Peter I and industrialization of the region.

Carbon accumulation

The mean long-term CAR (18.9±10.16 $g\,C\,m^{-2}\,a^{-1}$) fits well with the carbon accumulation rate of 18.6 $g\,C\,m^{-2}\,a^{-1}$ of northern peatlands (Yu *et al.* 2009). The value is slightly below the mean Holocene values of northern peatlands of 23±2 g C m^{-2} a^{-1} (Loisel *et al.* 2014) or 24.1 g C m^{-2} a^{-1} (Lavoie *et al.* 2005) and most comparable studies with a more local focus on the CAR (Table 2). The estimated CAR supports the suggestion of Payne *et al.* (2015) that the carbon accumulation rates of European Russian peatlands are close to the global average.

Long-term carbon accumulation is closely related to the climate due to its influence on primary production and decomposition (Clymo *et al.* 1992), increasing seasonality (Loisel *et al.* 2014) and changing vegetation composition (Clymo *et al.* 1998). The decrease in CAR at ~8 ka correlates well with a dry phase with establishment of Siberian birch forest-steppe. Dry conditions and possibly a lower water table might have prevented organic accumulation due to a higher decomposition rate.

A strong increase in peat accumulation rates and CAR from ~3.5 to 2.3 ka is noticeable. In vegetation development, this phase starts with a minimum of *Picea* and later *Ulmus* (Fig. 5), possibly indicating damage to the populations in the lowlands due to an increase in water level. The entire period is characterized by an increase in temperate arboreal taxa, testate amoebae and CAR, indicating at least regionally increasing summer temperatures and humid conditions in the area.

The following phase of reduced CAR between 2.3 and 1.3 ka is interpreted as a dry phase in the peat bog's development and corresponds to the phase of intensive anthropogenic activities in the area. Dry periods and intensifying anthropogenic pressure are known to adversely affect peat growth (McNeil & Waddington 2003; Lindsay 2010). Possibly both reasons play a role in the reduction in CAR. After the reduction in human impact and/or the increased water table after 1.3 ka there is a recovery of the peat bog and an increase in CAR.

The recent drainage appears to have resulted in low CAR as a consequence of increased decomposition in the top layer of the peat (Benavides 2014). Furthermore, an unstable water table and lack of moisture harm the growth of *Sphagnum* plants (McNeil & Waddington 2003) and therefore the productivity of organic material.

Conclusions

Our investigations on the sediment core Chernaya from Paltinskoe peat bog provide important insights into the vegetation, environmental and land-use history of the East European boreal forests in the mid-Kama region of the pre-Urals.

The pollen data show four major phases of the vegetation formation: (i) dominance of Siberian taiga and forest-steppe in the Early and the beginning of the Middle Holocene (8.8–6.9 ka), indicating a dry climate; (ii) spread of spruce and European broadleaved trees in the Middle Holocene (6.9–4 ka) under wetter climate conditions; (iii) the maximum extent of broadleaved trees coinciding with an arrival and spread of Siberian fir in the Late Holocene (4–2.3 ka); and (iv) a decline in broadleaved trees since the Early Iron Age (2.3 ka – present), possibly due to general climate cooling and timber extraction. We argue that temperate broadleaved trees might have spread from local refugia in the Urals, while Siberian fir arrived from the east and later spread further west.

The vegetation was strongly disturbed by fire in the Early Holocene, while from the Early Iron Age onwards, it was strongly influenced by anthropogenic deforestation, agricultural and pastoral activities. Four phases related to an increase in anthropogenic activities are reflected in the pollen diagram by the spread of *Artemisia*, other ruderal herbs, coprophilous fungal spores, the pioneer tree *Betula pubescens*-type and charcoal, which alternate with phases of recovery of spruce, pine and fir. The first phase between the 6th and 3rd centuries BCE corresponds to Ananyino culture, the second phase (1st–6th centuries CE) – Glyadenovo culture, the third phase (13th–15th centuries CE) – Rodanovo culture (?), and the last (18th–20th centuries CE) to Russian colonization. A phase in the 13th–15th centuries is still not documented archaeologically, highlighting a need for further investigations of the region.

The local development of the peat bog is characterized by non-gradual growth starting with a shallow lake with Cyperaceae-fern eutrophic peat and establishment of *Sphagnum* peat bog at 4.3 ka. The mean long-term carbon accumulation rate of 18.9±10.16 g C m^{-2} a^{-1} fits well with the carbon accumulation rate of northern peatlands. During *Sphagnum* bog development, a phase of intensive carbon accumulation with a rate of 18–53 g C m^{-2} a^{-1} occurred between 3.5 and 2.3 ka, indicating wet and warm conditions. The following dry phase correlates with a settlement phase of the Glyadenovo culture. A further and more detailed study of the Paltinskoe peat bog in relation to carbon fluxes, including more extensive sampling and direct measurement of carbon content, is important to better understand the developments in the region, especially in the context of future climate change and the estimation of potential carbon dioxide sinks.

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References

Anderson, D. E. 2002: Carbon accumulation and C/N ratios of peat bogs in North-West Scotland. *The Scottish Geographical Magazine 118*, 323–341.

Andreev, A., Tarasov, P. E., Ilyashuk, B. P., Ilyashuk, E. A., Cremer, H., Hermichen, W.-D., Wischer, F. & Hubberten, H.-W. 2005: Holocene environmental history recorded in Lake Lyadhej-To sediments, Polar Urals, Russia. *Palaeogeography, Palaeoclimatology, Palaeoecology 223*, 181–203.

Belavin, A. M. & Krylasova, N. B. 2008: *Drevnyaya Afcula: arkheologicheskiy komplex u s. Rozhdestvensk*. 603 pp. Permskiy Filial Instituta Istorii i Archeologii Uralskogo Otdeleniya Rossiyskoy Akademii Nauk, Perm.

van Bellen, S., Dallaire, P.-L., Garneau, M. & Bergeron, Y. 2011: Quantifying spatial and temporal Holocene carbon accumulation in ombrotrophic peatlands of the Eastmain region, Quebec, Canada. *Global Biogeochemical Cycles 25*, GB2016, https://doi.org/doi:10.1029/2010GB003877.

Benavides, J. C. 2014: The effect of drainage on organic matter accumulation and plant communities of high-altitude peatlands in the Colombian tropical Andes. *Mires and Peat 15*, 15 pp, http://www.mires-and-peat.net/.

Beug, H. J. 2004: *Leitfaden der Pollenbestimmung*. 542 pp. Verlag Dr. Friedrich Pfeil, München.

Blaauw, M. 2010: Methods and code for 'classical' age-modelling of radiocarbon sequences. *Quaternary Geochronology 5*, 512–518.

Blagoveshchenskiy, G. A. 1940: Ob iskopaemykh i sovremennykh torfyianikakh Srednego Zauralyia. *Sovetskaya Botanika 3*, 59–76.

Blagoveshchenskiy, G. A. 1943: Istoriya lesov vostochnogo sklona Srednego Urala. *Sovetskaya Botanika 6*, 3–16.

Bohn, U., Neuhäusl, R., Gollub, G., Hettwer, C., Neuhäuslová, Z., Schlüter, H. & Weber, H. 2003: *Map of the Natural Vegetation of Europe*. 655 pp. , Landwirtschaftsverlag, Münster.

Chambers, F. M., Beilman, D. W. & Yu, Z. 2011: Methods for determining peat humification and for quantifying peat bulk density, organic matter and carbon content for palaeostudies of climate and peatland carbon dynamics. *Mires and Peat 7*, 10 pp, http://www.mires-and-peat.net/.

Clymo, R. S., Foster, G. N., MacKay, J., Robertson, J., Shore, R. & Skidmore, D. I. 1992: Terrestrial biology in limed catchments. *In* Howells, G. & Dalziel, T. R. K. (eds.): *Restoring Acid Waters: Loch Fleet 1984–1990*, 331–361. Springer, Dordrecht.

Clymo, R. S., Turunen, J. & Tolonen, K. 1998: Carbon accumulation in peatlands. *Oikos 81*, 368–388.

Cremer, H., Andreev, A., Hubberten, H.-W. & Wischer, F. 2004: Paleolimnological reconstructions of Holocene environments and climate from Lake Lyadhej-To, Ural Mountains, northern Russia. *Arctic, Antarctic, and Alpine Research 36*, 147–155.

Danilova, M. M. 1948: Bolota doliny reki Kamy. *Izvestiya Estestvenno-nauchnogo Instituta pri Molotovskom gosudarstvennom Universitete im. Gor'kogo 12*, 253–268.

Degteva, S. V. & Dubrovskiy, Y. 2009: Raznoobrazie pikhtovykh lesov Pechoro-Ilychskogo zapovednika. *In* Ovesnov, S. A. (ed.): *Botanicheskie issledovaniya na Urale*, 95–100. Permskiy Gosudarstvenniy Universitet, Perm.

Demakov, D. A., Lychagina, E. L., Kopytov, S. V., Nazarov, N. N., Chernov, A. V., Trofimova, S. S., Lapteva, E. G. & Zaretskaya, N. E. 2016: Rekonstruktsiya prirodnogo okruzheniya drevnikh i srednevekovykh obshchestv v basseine verkhney Kamy. *In* Adaev, V.N., Matveeva, N.P., Riabogina, N.E. & Slepchenko, S.M. (eds.): *Materials of V International Conference "Ecology of ancient and traditional societies" 2016*, 92–97. Tiumen University, Tiumen.

Denisov, V. P., Melnichuk, V. F. & Mitryakov, A. E. 2011: Maloizuchennyi chronologicheskiy gorizont Zaosinovo VII-Nepryakha VII-Partizany IV epokhi bronzy Srednego Prikamya. *In* Viktorova, V. D. (ed.): *6e Bersovskie chteniya*, 107–116. Kvadrat, Ekaterinburg.

Elovicheva, Ya. K. 1991: Istoriya razvitiya prirodnoy sredy pozdne- i poslelednikovya Permskoy oblasti. *In* Shaporev, I. A. (ed.): *Karbonatnaya gazha SSSR*, 66–78. Izdatelstvo Permskogo Politekhnicheskogo Instituta, Perm.

Erdtman, G. 1960: The acetolysis method. *Svensk Botanisk Tidskrift 54*, 561–564.

van Geel, B. 1978: A palaeoecological study of Holocene peat bog sections in Germany and the Netherlands, based on the analysis of pollen, spores and macro- and microscopic remains of fungi, algae, cormophytes and animals. *Review of Palaeobotany and Palynology 25*, 1–120.

Gening, V. F. 1959: Mogilnik Kachka. *In* Kiselev, S. V. & Bader, O. N. (eds.): *Otchet Kamskoy (Votkinskoy) ekspeditsii*, 196–209. Akademiya Nauk SSSR, Moskva.

Gerasimov, D. A. 1926: Geobotanicheskoe issledovanie torfianykh bolot Urala. *Torfianoe Delo 3*, 53–58.

Gerasimov, D. A. 1932: *Torf, ego Proiskhozhdenie, Zaleganie i Rasprostranenie*. 67 pp. Gosnauktekhizdat, Moskva.

Gerasimov, I. P. (ed.) 1964: *Atlas Mira*. Akademiya Nauk SSSR-Glavnoe Upravlenie Geodezii i Kartografii SSSR, Moskva.

Goldina, R. D. 1999: *Drevnyaya i srednevekovaya istoriya udmurtskogo naroda*. 463 pp. Udmurtskiy Universitet, Izhevsk.

Golovchansky, G. P. & Melnichuk, A. F. 2014: *Drevnyaya i Srednevekovaya Istoriya Prikamya v Tsikle Ekskursionnykh Programm*. 222 pp. Perm University Press, Perm.

Golubeva, L. V. 1956: Rezultaty cporovo-pyltsevykh analizov ztkotorykh chetvertichnykh otlozheniy v Kishertskom rayone Molotovskoy oblasti. *Izvestiya Estestvenno-nauchnogo instituta pri Molotovskom gosudarstvennom universitete im. Gorkogo 13*, 175–190.

Gorchakovskiy, P. L. 1953: *Istoriya Razvitiya Rastitelnosti Urala*. 144 pp. Sverdlovskoe knizhnoe izdatelstvo, Sverdlovsk.

Gorchakovskiy, P. L. 1965: O sootnoshenii mezhdu gorizontalnoy i zonalnost'iu i vertikalnoy poyasnost'iu rastitelnogo pokrova na primere Urala i prilegayuschikh ravnin. *Trudy Instituta Biologii 42*, 3–32.

Heiri, O., Lotter, A. F. & Lemcke, G. 2001: Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. *Journal of Paleolimnology 25*, 101–110.

Henckel, A. A. 1974: Bolota Permskoy oblasti. *Biogeographiya i Kraevedenie 2*, 3–72.

Henckel, A. A. & Krasovsky, P. N. 1934: Materialy po izucheniyu rastitelnosti drevney terrasy r. Kamy i ee torfianykh bolot. *Bulletin de l'Institut des recherches biologiques de Perm 9*, 41–60.

Henckel, A. A. & Lebedeva, A. P. 1940: O vozraste torfianykh obnazheniy v alluviyakh Kamy. *Scientific Memoirs of the M. Gorki State University of Molotov 4*, 153–165.

Henriksen, M., Mangerud, J., Matiouchkov, A., Murray, A. S., Paus, A. & Svendsen, J. I. 2008: Intriguing climatic shifts in a 90 kyr old lake record from northern Russia. *Boreas 37*, 20–37.

Igoshina, K. N. 1927: Rastitel'nye soobshchestva na alluviyakh Kamy i Chusovoy. *Trudy BNII pri PGU 1*, 1–123.

Juggins, S. 2007: *C2 Version 1.5 User guide. Software for Ecological and Palaeoecological Data Analysis and Visualisation*. 73 pp. Newcastle University, Newcastle upon Tyne.

Kats, N. Ya. 1962: O lednikovykh ubezhishchakh i rasselenii shirokolistvennykh porod na Vostochno-Evropeyskoy ravnine v poslevaldayskoe vremia. *Bulleten Moskovskogo obshchestva ispytateley prirody, Otdelenie Biologii 57*, 52–63.

Kokarovtsev, V. K. 1992: *Resursy i Geologiya Golotsenovykh Agrokarbonatov Permskogo Preduralya*. 215 pp. Ekaterinburg, Uralgeologiya.

Korenyuk, S. N. 2009: K voprosu o datirovke nachalnogo etapa ananyinskoy kultury Volgo-Kamya. *Izvestiya Samarskogo nauchnogo tsentra RAN 2*, 265–270.

Korenyuk, S. N., Melnichuk, A. F. & Pereskokov, M. L. 2018: Vozniknovenie i razvitie proizvodyashchey ekomomiki v taezhnoy zone Srednego Priuralya (pozdniy eneolit – nachalo rannego srednevekovya). *In* Chernykh, I. N. (ed.): *Tverskoy Archaeologicheskiy Sbornik*, 18–30. Triada, Tver.

Koryakova, L. & Epimakhov, A. V. 2007: *The Urals and Western Siberia in the Bronze and Iron Ages*. 383 pp. Cambridge University Press, Cambridge.

Krylov, G. V., Maradudin, I. I., Mikheev, N. I. & Kozakova, N. F. 1986: *Pikhta*. 240 pp. Agropromizdat, Moscow.

Kultti, S. 2004: *Holocene changes in treelines and climate from Ural Mountains to Finnish Lapland*. PhD Dissertation, 33 pp. University Printing House, Helsinki.

Lapteva, E. G. & Korona, O. M. 2012: Holocene vegetation changes and anthropogenic influence in the forest-steppe zone of the Southern Trans-Urals based on pollen and plant macrofossil records from the Sukharysh cave. *Vegetation History and Archaeobotany 21*, 321–336.

Lapteva, E. G., Krylasova, N. B. & Sarapulov, A. N. 2016: Rezultaty palinologicheskogo izucheniya otlozheniy Rozhdestvenskoe gorodishche (2015). *Vestnik Permskogo Nauchnogo Centra 3*, 15–22.

Lapteva, E. G., Sarapulov, A. N. & Krylasova, N. B. 2019: Rozhdestvenskoe gorodishche: itogi palinologicheskikh issledovaniy. *Trudy Kamskoy Arkheologo-Etnograficheskoy Ekspeditsii Permskogo Gosudarstvennogo Gumanitaarno-Pedagogicheskogo Universiteta 15*, 25–33.

Lapteva, E. G., Zaretskaya, N. E., Kosintsev, P. A., Lychagina, E. L. & Chernov, A. V. 2017: First data on the middle to late Holocene dynamics of vegetation in the Upper Kama region. *Russian Journal of Ecology 48*, 326–334.

Lavoie, M., Paré, D. & Bergeron, Y. 2005: Impact of global change and forest management on carbon sequestration in northern forested peatlands. *Environmental Reviews 13*, 199–240.

Lindsay, R. 2010: *Peatbogs and Carbon: A Critical Synthesis to Inform Policy Development in Oceanic Peat Bog Conservation and Restoration in the Context of Climate Change*, 315 pp.. University of East London, London.

Loisel, J., Yu, Z., Beilman, D., Camill, P., Alm, J., Amesbury, M. J., Anderson, D., Andersson, S., Bochicchio, C., Barber, K., Belyea, L. R., Bunbury, J., Chambers, F. M., Charman, D. J., De Vleeschouwer, F., Fiakiewicz-Kozie, B., Finkelstein, S. A., Gaka, M., Garneau, M., Hammarlund, D., Hinchcliffe, W., Holmquist, J., Hughes, P., Jones, M. C., Klein, E. S., Kokfelt, U., Korhola, A., Kuhry, P., Lamarre, A., Lamentowicz, M., Large, D., Lavoie, M., MacDonald, G., Magnan, G., Mðkilð, M., Mallon, G., Mathijssen, P., Mauquoy, D., McCarroll, J., Moore, T. R., Nichols, J., O'Reilly, B., Oksanen, P., Packalen, M., Peteet, D., Richard, P. J. H., Robinson, S., Ronkainen, T., Rundgren, M., Sannel, A. B. K., Tarnocai, C., Thom, T., Tuittila, E.-S., Turetsky, M., Vðliranta, M., van der Linden, M., van Geel, B., van Bellen, S., Vitt, D., Zhao, Y. & Zhou, W. 2014: A database and synthesis of northern peatland soil properties and Holocene carbon and nitrogen accumulation. *The Holocene 24*, 1028–1042.

Lychagina, E. L., Zaretskaya, N. E. & Mitroshin, E. N. 2017: Novye dannye o khronologii kamskoy mezoliticheskoy kultury. *In* Derevianko, A. P. & Tishkin, A. A. (eds.): *Materials of the V (XXI) Russian Archaeological Congress*, 640–641. Altai University, Barnaul.

Maslennikova, A. V., Udachin, V. N. & Aminov, P. G. 2016: Lateglacial and Holocene environmental changes in the Southern Urals reflected in palynological, geochemical and diatom records from the Lake Syrytkul sediments. *Quaternary International 420*, 65–75.

McNeil, P. & Waddington, J. M. 2003: Moisture controls on *Sphagnum* growth and CO_2 exchange on a cutover bog. *Journal of Applied Ecology 40*, 354–367.

Melnichuk, A. F., Bordinskih, G. A., Mokrushin, V. P., Degtyareva, M. I. & Lychagina, E. L. 2001: Novye pozdnemezoliticheskie i ranneneoliticheskie pamyatniki v Verhnem i Srednem Prikam'e. *In* Melnichuk, A. F. (ed.): *Arkheologiya i etnografiya Srednego Priural'ya*, 142–161. Perm University Press, Berezniki.

Melnichuk, A. F., Korenyuk, S. N., Pereskokov, M. L. & Tretyakov, D. V. 2011: Novye paleoliticheskie mestonakhozhdeniya kostenkovsko-streletskogo tipa v Permskom Priulalye. *In* Melnichuk, A. F., (ed.): *Materials of conference "Economico-pravovye, socialno-politicheskie i kulturno-istoricheskie aspekty razvitiya regionov"*, 401–403. Perm University Press, Berezniki.

Moore, P. D., Webb, J. A. & Collinson, M. E. 1999: *Pollen Analysis.* 216 pp. Blackwell Science, Oxford.

Nemkova, V. K. 1992: Flory i rastitel'nost' Preduralyia v pliotsene, pleistotsene i golotsene. *In* Yakhimovich, V. L., Nemkova, V. K., Latypova, E. K., Popova-Lvova, M. G., Yakovlev, A. G., Ismagilova, G. M. & Suleimanova, F. I. (eds.): *Flora i Fauna Kainozoya Preduralyia i Nekotorye Voprosy Magnitostratigrafii*, 11–32. Bashkirskiy Nauchniy Tsentr Uralskogo Otdeleniya Rossiyskoy Akademii Nauk, Ufa.

Novenko, E. Yu, Tsyganov, A. N., Pisarchuk, N. M., Volkova, E. M., Babeshko, K. V., Kozlov, D. N., Shilov, P. M., Payne, R. J., Mazei, Y. & Olchev, A. V. 2018: Forest history, peatland development and mid- to late Holocene environmental change in the southern taiga forest of central European Russia. *Quaternary Research 89*, 223–236.

Novenko, E. Yu, Tsyganov, A. N., Volkova, E. M., Kupriyanov, D. A., Mironenko, I. V., Babeshko, K. V., Utkina, A. S., Popov, V. & Mazei, Y. 2016: Mid- and Late Holocene vegetation dynamics and fire history in the boreal forest of European Russia: a case study from Meshchera Lowlands. *Palaeogeography, Palaeoclimatology, Palaeoecology 459*, 570–584.

Novenko, E. Yu, Volkova, E. M., Nosova, N. B. & Zuganova, I. S. 2009: Late Glacial and Holocene landscape dynamics in the southern taiga zone of East European Plain according to pollen and macrofossil records from the Central Forest State Reserve (Valdai Hills, Russia). *Quaternary International 207*, 93–103.

Oborin, V. A. 1962: Raskopki pamyatnikov zheleznogo veka v Verkhnem i Srednem Prikamye. *Voprosy arkheologii Urala 2*, 95–100.

Ovesnov, S. A. 2009: *Mestnaya Flora: Flora Permskogo Kraya i ee Analiz*. 172 pp. Permskiy gosudarstvenniy universitet, Perm.

Panait, A., Diaconu, A., Gałka, M., Grindean, R., Hutchinson, S. M., Hickler, T., Lamentowicz, M., Mulch, A., Tanţău, I., Werner, C. & Feurdean, A. 2017: Hydrological conditions and carbon accumulation rates reconstructed from a mountain raised bog in the Carpathians: a multi-proxy approach. *Catena 152*, 57–68.

Panova, N. K. & Antipina, T. G. 2016: Late Glacial and Holocene environmental history on the eastern slope of the Middle Ural mountains, Russia. *Quaternary International 420*, 76–89.

Panova, N. K., Antipina, T. G. & Jankovska, V. 2010: Holocene history of the environment and development of bogs on the eastern slope of the polar and pre-polar Urals (Russia). *Environmental Dynamics and Global Climate Change 1*, 8–22.

Pavlov, P. Yu 2013: Drevneishee proshloe Permskogo kraya: paleolit. *Vestnik Permskogo Nauchnogo Centra 4*, 22–32.

Payne, J. K., Malysheva, E., Tsyganov, A., Pampura, T., Novenko, E., Volkova, E., Babeshko, K. & Mazei, Y. 2015: A multi-proxy record of Holocene environmental change, peatland development and carbon accumulation from Staroselsky Moch peatland, Russia. *The Holocene 26*, 314–326.

Pereskokov, M. L. 2013: Territoriya i lokalnye varianty pozdnego etapa glyadenovskoy kultury v Permskom Prikamye. *Vestnik Permskogo Universiteta. Seriya Istoriya 1*, 58–66.

Pereskokov, M. L. 2018: *Permskoe Priuralye v Finale Rannego Zheleznogo Veka*. 320 pp. State University Press, Perm.

Pidek, I. A., Svitavská-Svobodová, H., van der Knaap, W. O. & Magyari, E. 2013: Pollen percentage thresholds of *Abies alba* based on 13-year annual records of pollen deposition in modified Tauber traps: perspectives of application to fossil situations. *Review of Palaeobotany and Palynology 195*, 26–36.

Polyakov, Y. Yu 1967: Itogi izucheniya pamyatnikov glyadenovskoy kultury v Verkhnem i Srednem Prikamye. *Uchenye zapiski PGU 148*, 197–215.

Polyakov, Y. 2001: Glyadenovskaya cultura. *In* Melnichuk, A. F. (ed.): *Arkheologiya i etnografiya Srednego Priural'ya*, volume *1*, 10–19. Perm University Press, Berezniki.

Ponomarev, A. N. 1948: Lesostepnoy kompleks severnoy okrainy Kungurskoy lesostepi. *Izvestiya Estestvenno-Nauchnogo Instituta pri Molotovskom Universitete 12*, 225–233.

Poska, A. & Pidek, I. A. 2010: Pollen dispersal and deposition characteristics of *Abies alba, Fagus sylvatica* and *Pinus sylvestris*, Roztocze region (SE Poland). *Vegetation History and Archaeobotany 19*, 91–101.

R Core Team. (2020): R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Reimer, P. J., Bard, E., Bayliss, A., Beck, J. W., Blackwell, P. G., Bronk Ramsey, C., Buck, C. E., Cheng, H., Edwards, R. L., Friedrich, M., Grootes, P. M., Guilderson, T. P., Haflidason, H., Hajdas, I., Hatt, C., Heaton, T. J., Hogg, A. G., Hughen, K. A., Kaiser, K. F., Kromer, B., Manning, S. W., Niu, M., Reimer, R. W., Richards, D. A., Scott, E. M., Southon, J. R., Turney, C. S. M. & van der Plicht, J. 2013:

IntCal13 and Marine13 radiocarbon age calibration curves, 0–50,000 years cal BP. *Radiocarbon 55*, 1869–1887.

Schmidt, A. V. 1927: Kacka. Beiträge zur Erforschung der Kulturen Ostrusslands in der Zeit der Völkerwanderung (III.-V. Jh.). *Eurasia Septentrionalis Antiqua 1*, 18–50.

Shklyaev, V. A. & Shklyaeva, L. S. 2006: Klimaticheskie resursy Uralskogo Prikamiya. *Geographical. Bulletin 2*, 97–110.

Shumilovskikh, L. S., Schlütz, F., Achterberg, I., Kvitkina, A., Bauerochse, A. & Leuschner, H. H. 2015: Pollen as nutrient source in Holocene ombrotrophic bogs. *Review of Palaeobotany and Palynology 221*, 171–178.

Stobbe, A., Gumnior, M., Röpke, A. & Schneider, H. 2015: Palynological and sedimentological evidence from the Trans-Ural steppe (Russia) and its palaeoecological implications for the sudden emergence of Bronze Age sedentarism. *Vegetation History and Archaeobotany 24*, 393–412.

Stockmarr, J. 1971: Tablets with spores used in absolute pollen analysis. *Pollen et Spores 13*, 615–621.

Storozheva, M. M. 1962: O vozraste pervoy nadpoymennoy terrasy doliny reki Kamy, po dannym analiza pyltsy v torfe. *Zapiski Sverdlovskogo otdeleniya Vsesoiuznogo botanicheskogo obshchestva 2*, 115–123.

Sukachev, V. N. & Poplavskaya, G. I. 1946: Ocherk istorii ozer i rastitel'nosti srednego Urala v techenie golotsena po dannym izucheniya sapropelevykh otlozheniy. *Bulletin of Commission for Quaternary Research 8*, 5–37.

Svendsen, J. I., Krüger, L. C., Mangerud, J., Astakhov, V. I., Paus, A., Nazarov, D. & Murray, A. 2014: Glacial and vegetation history of the Polar Ural Mountains in northern Russia during the Last Ice Age, Marine Isotope Stages 5–2. *Quaternary Science Reviews 92*, 409–428.

Tartakovskiy, A. M. (ed.) 2012: *Atlas Permskogo Kraya*. 124 pp. Permskiy Gosudarstvenniy Natsionalniy Issledovatelskiy Universitet, Perm.

Tolonen, K. & Turunen, J. 1996: Accumulation rates of carbon in mires in Finland and implications for climate change. *The Holocene 6*, 171–178.

Trofimova, S. S., Krylasova, N. B. & Sarapulov, A. N. 2016: Arkheobotanicheskie issledovaniya srednevekovogo Rozhdestvenskogo gorodishcha (Permskiy kray). *Vestnik Permskogo Nauchnogo Centra 3*, 23–29.

Verkhoyarov, G. N. (ed.) 1976: *Torfyanye Mestorozhdeniya Permskoy Oblasti*. 403 pp. Geoltorfrazvedka, Moskva.

Vybornov, A. A., Lychagina, E. L., Vasilyeva, I. N., Melnichuk, A. F. & Kulkova, M. A. 2019: Novye dannye o periodizatsii i khronologii novoilyinskikh, garinskikh i borskikh pamyatnikov Prikamya. *Vestnik Permskogo Universiteta. Seriya Istoriya 1*, 34–47.

Yu, Z., Beilman, D. W. & Jones, M. C. 2009: Sensitivity of Northern Peatland Carbon Dynamics to Holocene Climate Change. *In* Baird, A. J., Belyea, L. R., Comas, X., Reeve, A. S. & Slater L. D. (eds.): *Carbon Cycling in Northern Peatlands. Geophysical Monograph Series 184*, 55–69. AGU, Washington, D. C.

Zaretskaya, N. E., Lychagina, E. L., Lapteva, E. G., Trofimova, S. S. & Chernov, A. V. 2020: Poima Kamy: rekonstruktsiya sredy obitaniya drevnikh i srednevekovykh soobshchestv srednego Preduralya. *Rossiyskaya Archeologiya 1*, 44–58.